

Void Entry by *Aedes aegypti* (Diptera: Culicidae) Mosquitoes Is Lower Than Would Be Expected by a Randomized Search

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Abstract

Insects enter every passable space on the planet. Despite our best efforts, flying insects infiltrate slightly open windows in domiciles, automobiles, storage spaces, and more. Is this ubiquitous experience a consequence of insect abundance and probability, or are flying insects adept at detecting passageways? There remains a lack of understanding of insect effectiveness in finding passage through the voids and imperfections in physical barriers in response to attractants, a topic particularly critical to the area of insect-borne disease control. In this study, we recorded the passage of *Aedes aegypti* mosquitoes through voids in vertically oriented bed net fabrics within a cylindrical flight arena. We model the probability mosquitoes will discover and navigate the void in response to a physical attractant by observing their search behavior and quantifying the region within a void that is physically navigable, constrained by body size. Void passage rates were lower than that would be expected by purely randomized search behaviors and decline rapidly as the void diameter approaches the in-flight width of the insect.

Key words: insect flight, disease control, insect control, insect sensing, probability

The understanding of how insects detect and enter voids in physical barriers is relevant to entomology and insect control, and may provide the latest generations of flying vehicles an enhanced ability to do the same. Physical separation barriers, such as bed nets, tents, walls, and clothing, are ubiquitous examples how humans worldwide separate themselves from insects. However, physical barriers are rarely perfect due to flaws or openings that provide passage for flying insects over a great range of length scales. The Empress cicada, *Megapomponia imperatorial* Westwood (Hemiptera: Cicadidae), has a wingspan of approximately 20 cm, while the fairy fly wasp, *Kikiki huna* Huber (Hymenoptera: Mymaridae), has a wingspan of less than 0.3 mm (Sane 2016). Although insect flight has been the subject of study for decades (Wang 2005), little is known about the physical mechanisms and probabilities that govern insect navigation of voids in physical structures. Insects that frequently enter hives and flowers, such as wasps and bees (Dyer and Could 1983, Getz and Akers 1994, Seeley 2009, Chakravarthi et al. 2016), are particularly adept at navigating small openings, synthesizing visual, olfactory, and heat sensing to find their target. In these instances, entering a hive or flower, the insect has been programmed by evolution to find the small void effectively. However, the built world provides insects with a large variety of unusual obstacles to maneuver.

Mosquitoes are an ideal model organism for the first studies into void navigation, for they are readily excited in captivity (Dickerson et al. 2012, 2015; Dickerson and Hu 2014; Sutcliffe and Colborn 2015; Sutcliffe et al. 2017), and probe physical barriers for entry in response to olfactory and thermal attractants. Discoveries of mosquito navigation of voids is particularly important to scientists studying mosquito-borne disease control. Billions of people worldwide rely on bed nets for protection against diseases (Guerra et al. 2008, Tolle 2009) such as malaria, dengue, chikungunya, and Zika. While very effective when new, bed nets are susceptible to rips and tears (Lengeler 2004, Kitchen et al. 2009, Sutcliffe et al. 2017), loss of insecticidal potency with age, and increasing insecticide resistance (Toé et al. 2014). An example of void entry in a bed net is presented in Fig. 1. In contrasting scenarios, the negotiation of an orifice in a barrier is desirable, such as the openings on insect traps (Hoel et al. 2011, Peña Torres et al. 2016). In all instances, mosquitoes are attracted to an odor source beyond the barrier (Takken 1991). The probability a mosquito, or any other insect, can enter a void of particular shape and size is not well-understood.

In similar studies (Sutcliffe and Colborn 2015, Sutcliffe et al. 2017) to that presented here using a common malaria mosquito *Anopheles (An.) gambiae* Giles (Diptera: Culicidae), researchers recorded bed net entry by mosquitoes using arenas found a

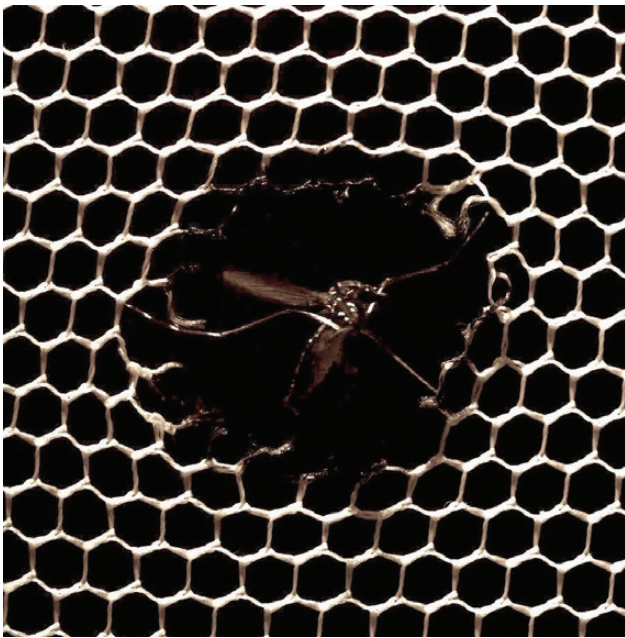


Fig. 1. *Ae. aegypti* mosquito flying through a 9-mm diameter void in a bed net.

positive correlation between void area and void passage probability. Mosquito appearance at voids is well predicted by the void area and perimeter for tests using full-scale bed nets (Sutcliffe et al. 2017). Mosquitoes constrained to flight arenas had greater success defeating nets with smaller arenas and larger voids (Sutcliffe and Colborn 2015) and were more likely to enter voids that were on the floor of the arena, such that the attractant lay beneath. Missing from literature is a statistical model that employs insect size and void size to predict probability of passage, and one that explores the limits of voids which can be entered in flight. This study seeks to fill these gaps, introduce behavioral data for another mosquito species, *Aedes aegypti* (Linnaeus) (Diptera: Culicidae), and trial a range of void sizes closer to the size of in-flight mosquitoes.

In this study, we investigated the ability of mosquitoes to enter circular voids within insecticide-free bed net fabric in response to a human mimicking attractant. In the Materials and Methods section, we describe our experimental methods and protocol for mosquito care. We present experimental data, data analysis, and probabilistic modeling in the Results section. Implications of our work and avenues for future research are discussed in the Discussion section.

Materials and Methods

Mosquito Acquisition and Care

Ae. aegypti mosquitoes were provided by Dr. Bradley Willenberg at the University of Central Florida's College of Medicine as newly eclosed adults and housed in a humid incubator at 26°C. The mosquitoes were fed a solution of sucrose and water via a cotton ball and were never bloodfed. Mosquitoes were used in experiments within 1-wk of receipt.

Void Passage Trials

The flight arena shown in Fig. 2 was formed by three 305-mm (1-ft) segments of optically clear acrylic tubing with an inner diameter $D_a = 165$ mm, sourced from McMaster-Carr (Atlanta, GA). Mosquitoes were placed in the flight arena using aspirators, approximately 20 per trial. A void-free net (not pictured) separated

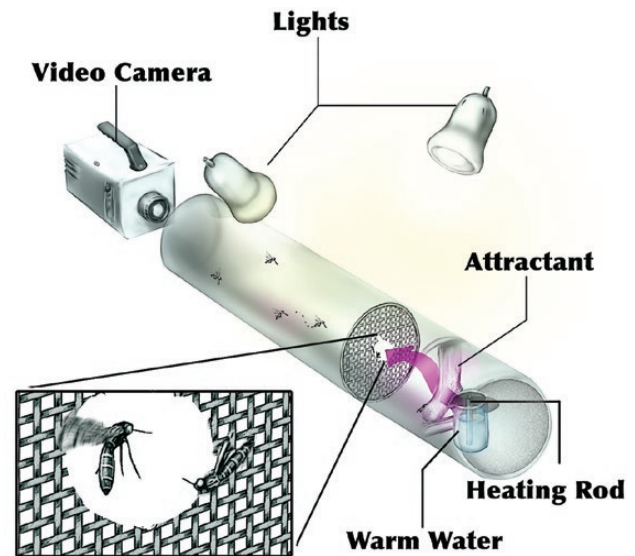


Fig. 2. Experimental flight arena.

the mosquitoes from the flawed bed net barrier from Livingstone Supply Co. (Johannesburg, South Africa). The net is made from polyester and has a hexagonal mesh. Each hexagon measures 1.5 mm across and net fibers bundles are coiled together to form 200 μ m diameter strands. A photograph of the net mesh is provided in Suppl Fig. 1 (online only). Voids were cut into the net with a laser engraving machine. During laser cutting, the net was sandwiched between two 3.2-mm (1/8-inch) sheets of plywood which acts to arrest the flame generated by the laser and ensures an accurate cut. A 20-mm void in a net and in an acrylic sheet manufactured using a laser cutter can be seen in Suppl Fig. 2 (online only) and shows the efficacy of our method. Void diameters D and areas ($\pi D^2 / 4$) were inferred from these programmed cuts and verified with digital calipers. Therefore, the circumference of the void is taken to be circle drawn by the terminated mesh fibers and does not include the space between them. The carbonization of the net fibers by the laser can be seen in Fig. 1.

A human-mimicking attractant was present when mosquitoes entered the tube, whom were given 3 min to acclimate to the tube before the void-free net was removed at the beginning of the trial. The attractant consisted of a sock worn for at least 12 h, always from the same individual, and a beaker of water maintained at 35°C by a rod heater. The sock was replaced every hour. These items together provide the scent, heat, and humidity expelled by a human. Scent from the attractant is allowed to freely diffuse through the net with no forced airflow. Voids were placed concentric to the outer tube. Insects were filmed with a Nikon 810D at 30 fps to keep record of barrier entry times and flight tracks. No additional lighting beyond fluorescent ceiling lighting was provided for entry trials. Mosquitoes were anesthetized with CO₂ upon trial conclusion and discarded. High-speed videos provided as Suppl Movies (online only) were filmed with a Photron AX-100 (Tokyo, Japan) at 250–500 fps and lit by a GS Vitex (Bad Soden Salmünster, Germany) white 24-LED lamp head.

Measurements and Calculations

Mosquito counts taken from videos were used to generate a passage success rate $E_r = (\text{number of void passages})/N$ for each void size. The in-flight width $w = 10.6 \pm 0.90$ mm, $N = 3$, of our *Ae. aegypti* mosquitoes was measured from video using Tracker. We note that this is not a fixed dimension per individual, as legs may shift in flight.

Curve fitting to data was performed with MATLAB (Mathworks, Natick, MA) using the non-linear least square method.

Results

Void Passage Rates

We placed nonanesthetized, nonbloodfed female *Ae. aegypti* mosquitoes in a horizontal, circular tube with a compromised barrier at one end, as shown in Fig. 2. The barrier was insecticide-free mosquito bed net fabric (Fig. 1) with manufactured voids of varying diameters D , listed in Table 1, cut into the net and placed concentric to the tube. Over the time course of 10 min mosquitoes were permitted to attempt passage through the barrier. Trials were performed with approximately 20 individual mosquitoes and repeated until $N = 100$ individuals were exposed to each barrier condition. We did not observe intra-specific interaction during trials or within the cups used to house mosquitoes, nor were such interactions reported by a previous study (Sutcliffe et al. 2017). Individuals were always separated by gender. Through video analysis, we recorded the time each void passage occurred.

A timeline of escapes is presented in Fig. 3a. As expected, mosquitoes found passage through larger voids more quickly and at greater numbers, but the success rate E_r of entering a breach was not linearly proportional with area A for the ten void sizes tested, as shown in Fig. 3b, particularly as the diameter of the void approached $w \approx 10$ mm. Likewise, the number of mosquitoes capable of entering the flaws decreased dramatically for voids smaller than 10 mm ($E_r = 42\%$). A 9-mm void permitted $E_r = 15\%$, while the 8-mm void permitted $E_r = 0$ over the time course of 10 min. To examine whether passage through the smallest voids was at all possible, we performed a 1-h trial for 8- and 9-mm voids. Over the course of the 1-h attempt, only 1 of 100 mosquitoes found its way through the 8-mm void, whereas $E_r = 17\%$ for the 9-mm void, as shown by the timeline in Fig. 3c.

Movement Across Barriers

For four trials with a reduced number of mosquitoes in the arena, we trained a camera concentric with the flight arena, as shown in Fig. 2, and tracked individual mosquito movements as they probed the barrier in response to the olfactory attractant. These escape trials are not included in the calculations of E_r above. Two such mosquito tracks from entry into the flight arena at $t = 0$ s through $t = 180$ s, or void passage if sooner, are shown in Fig. 4. The leftmost plots in Fig. 4 show a two-dimensional path, with waypoints gathered every second, and not corresponding to net contact. The individual in Fig. 4a did not complete passage through the 10-mm diameter void during the test period of 180 s despite a high level of activity.

Table 1. Entry rate and probability values for 10-min entry trials.

D (mm)	E_r (%)	ZO/A $_p$	C (s $^{-1}$)	R^2
8	0	0.132	0	1.00
8.5	1	0.171	0.014	0.494
9	15	0.213	0.145	0.955
10	41	0.311	0.309	0.959
13	39	0.617	0.123	0.987
15	47	0.849	0.131	0.978
18	39	1.25	0.070	0.928
20	53	1.56	0.098	0.894
25	56	2.46	0.064	0.932
30	60	3.56	0.049	0.922

In contrast, the individual in Fig. 4b was by comparison not as active, but did pass through the 20-mm diameter void at $t = 175$ s. We provide additional tracks of mosquito movement in Suppl Figs. 3 and 4 (online only). Considering all mosquitoes tracked,

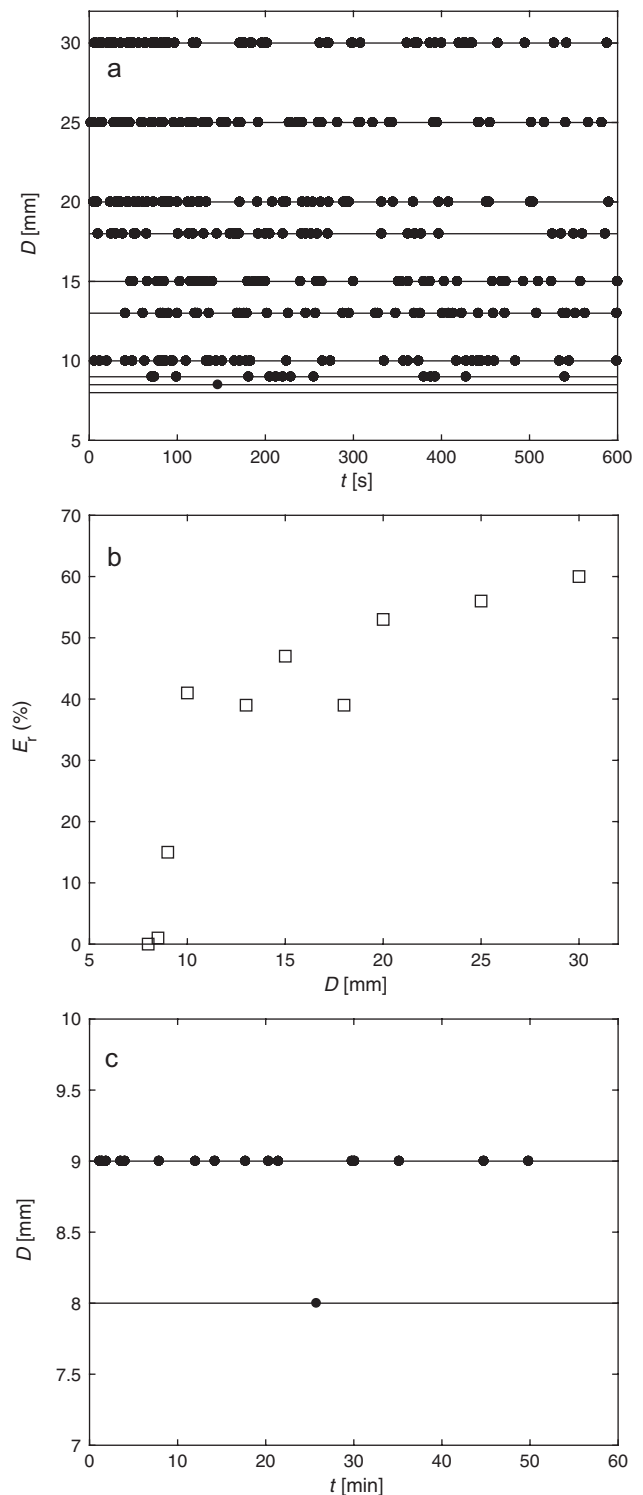


Fig. 3. Plots showing (a) a timeline of mosquito entry through voids of varying size over the time course of 10 min, where a single dot represents a single entry event, (b) the percentage of 100 mosquitoes that passed through each void within 10 min, and (c) a timeline for mosquito entry through 8- and 9-mm diameter voids within 1 h.

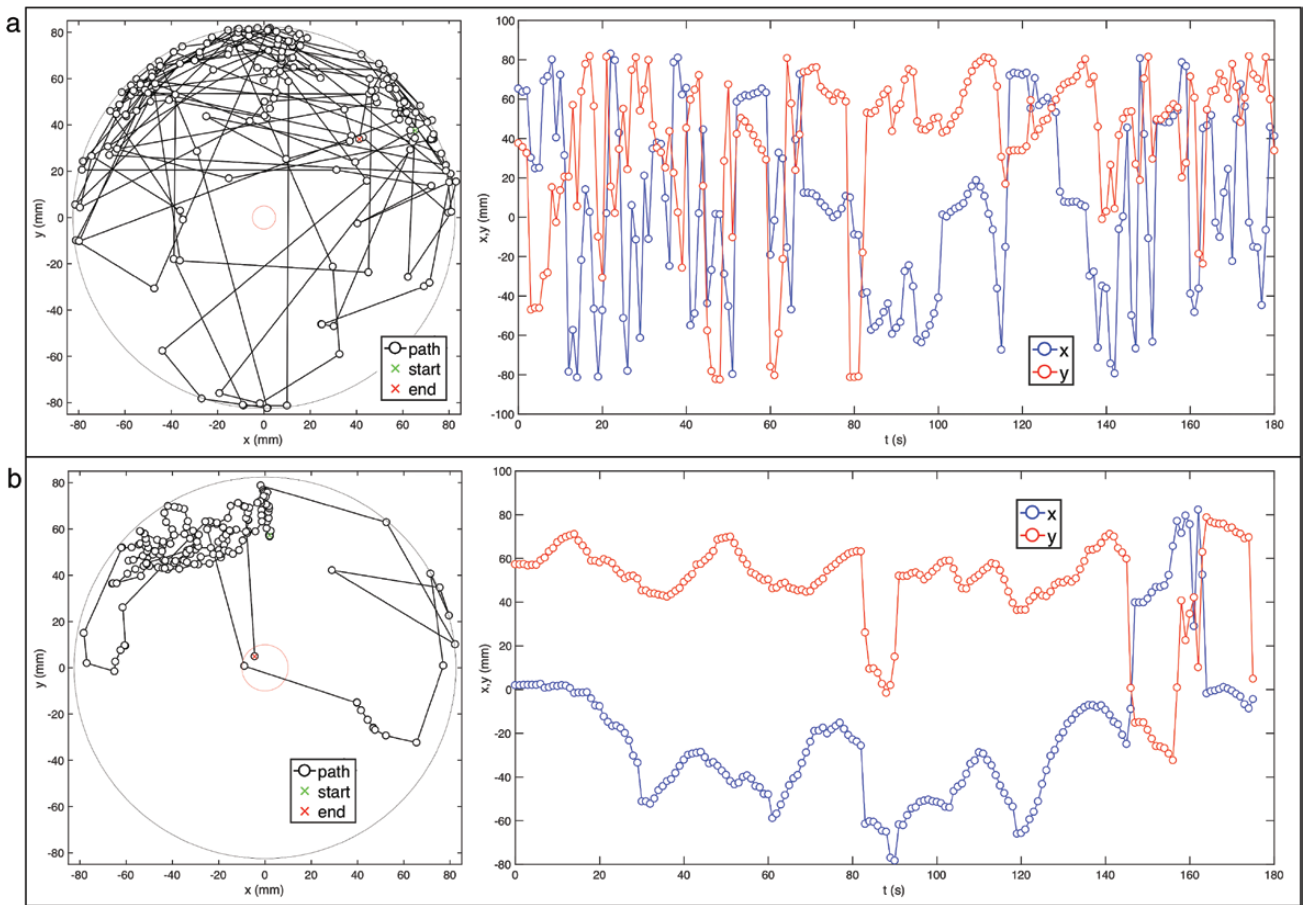


Fig. 4. Two-dimensional tracks of mosquito position in the flight area. The leftmost plots a view normal to the net barrier as mosquitoes probe different points on the net for passage. A single marker is plotted in 1-s intervals for 3 min. The rightmost plots show temporal x - and y -positions of the mosquito tracks. A 10- and 20-mm diameter voids were used in (a) and (b), respectively.

there appears to be no pattern or strategy for probing a physical barrier, but instead mosquitoes display a high degree of randomness in flight direction. The randomness in these searches is difficult to quantify because randomness quantification methods rely on a number sequences for computation (Leshner and Pfaff 2011), and such methods would be rendered invalid by the slight error in position measurement. However, we may assign sinuosity values to the successful mosquitoes to quantify their efficacy. The sinuosity of individual in Fig. 4b, $S_b = 20.4$, while that of Fig. 4a cannot be calculated because the mosquito did not find the hole within the allotted time, but we know that $S_a > 82.8$. We note that finer temporal resolution in tracking would more faithfully represent mosquito motion and yield greater S values. Such high values indicate the mosquito is unable to sense the hole directly.

Zone of Acceptance

Prior to discussion of the probability a mosquito will defeat a void in a physical barrier, it is imperative to define the areas through which a mosquito may occupy and pass. A mosquito's center of mass (COM) may only be found within a certain portion of the flight arena due to outstretched leg collisions with the arena walls in flight. This region of possible occupation by the COM across the plane formed by the barrier is shown by the white and green areas shown in Fig. 5a, assuming outstretched legs act as rigid members. We model the mosquito as a rigid stick of length $w = 10$ mm, as shown by the blue bars in Fig. 5c and d. This assumption of rigid body flight is supported by Suppl Movie 1 (online only). The possible occupancy area A_p

92.3% the cross-sectional area of the flight arena, determined by finding the area shared by two overlapping circles of diameter D_a with center offset of w . Accordingly,

$$A_p = \frac{D_a}{2} \cos^{-1} \left(\frac{w}{D_a} \right) - \frac{1}{2} w \sqrt{D_a^2 - w^2}. \quad (1)$$

The portion within the void a mosquito may pass we dub the zone of acceptance (ZOA). In a previous study (Sutcliffe and Colborn 2015), the authors report an 'edge effect' such that as void area doubles, entry rates *An. gambiae* do not increase accordingly due to mosquito interaction with void edges. We found comparable outcomes, and in our observations mosquitoes can enter voids when their COM, aligned with the head, is within the void and if only one or fewer of their two most outstretched legs collides with the barrier (see Suppl Movies 1 and 2 [online only]). This is analogous to a slender rod falling onto a horizontal plane containing a circular void. When the rod's COM coincides with the voided space and it can rotate about a void's edge, it will pass through. Likewise, no collision of the COM with the barrier permits passage. The ZOA is formed two circles with diameter equivalent to that of the void, D , with centers offset $-w/2$ and $w/2$ horizontally from the void center. The area of overlap of these circles and the void circle can be determined by

$$\text{ZOA} = D^2 \left[\cos^{-1} \frac{w}{2D} - \frac{1}{2} \cos^{-1} \frac{w}{D} \right] + \frac{w}{2} \left[\sqrt{D^2 - w^2} - \sqrt{D^2 - \frac{w^2}{4}} \right], \quad (2)$$

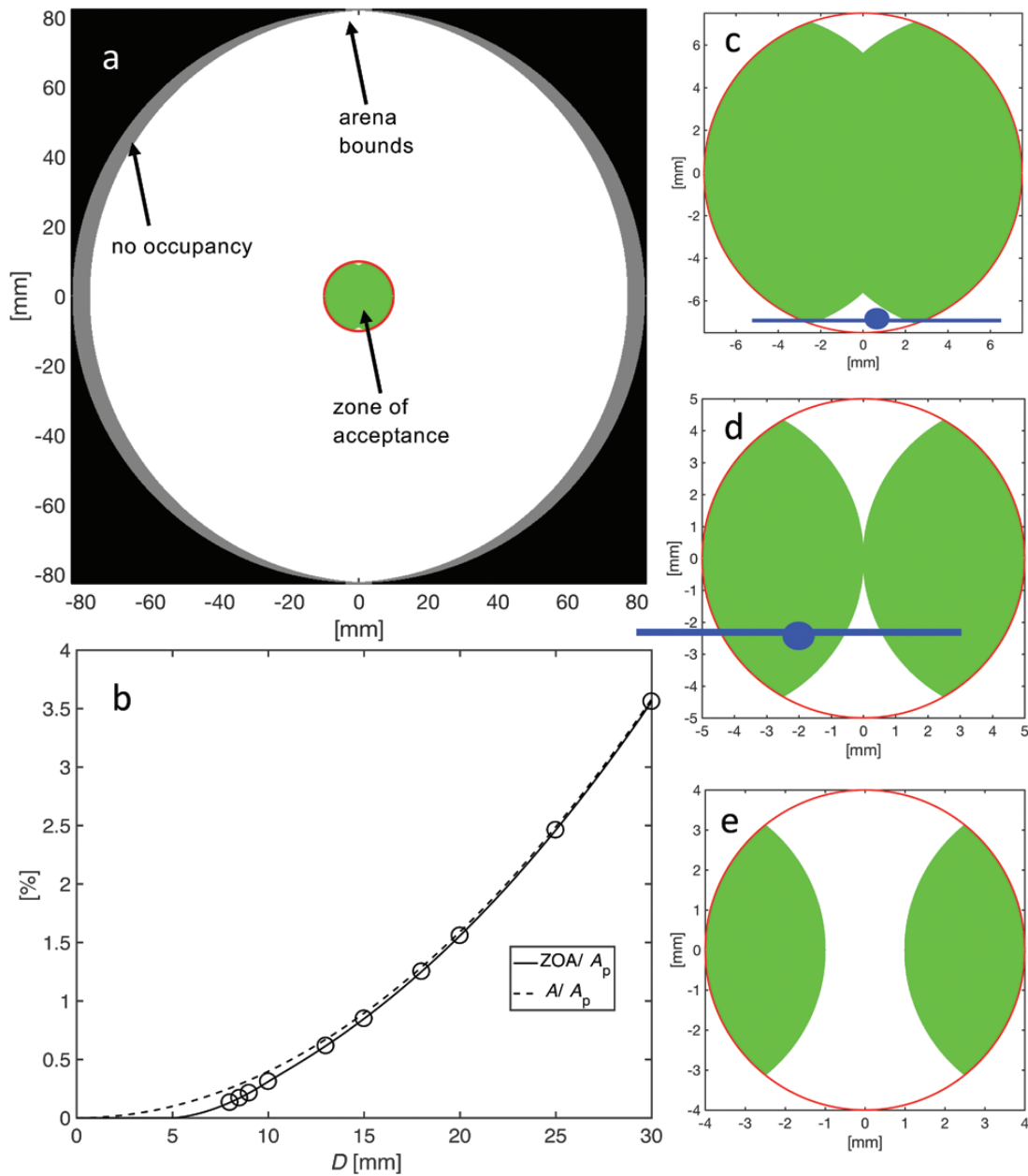


Fig. 5. The diagram in (a) marks the zones a mosquito may probe to pass through the barrier (ZOA) and the area they cannot occupy. In (b), $p = ZOA / A_p$ and A / A_p are plotted versus void diameter D , with an inset zoom box for the leftmost values on the curves. The plots in (c–e) show the shapes of the ZOA inside 13-, 8-, and 6-mm voids, respectively. The blue bars in (c) and (d) represent a model mosquito interacting with the ZOA. The mosquito in (c) would be permitted passage, whereas the mosquito in (d) would not.

which is robust to mosquito roll and pitch. Roll will only rotate the zones in Fig. 5a, c–e but has no effect on the magnitude of ZOA. The change in flight pitch likewise has no effect on the ZOA.

The ratio $p = ZOA / A_p$ is plotted in Fig. 5b. For the larger voids, the ZOA nearly coincides with the void area A , but as D decreases, the ZOA relative to A likewise decreases, as shown in Fig. 5c–e. For voids with $D < w$, the void centerpoint no longer lies within the ZOA, like that shown in Fig. 5e, and the mosquito must place its COM eccentric to the void to complete passage. Voids with $D < w / 2 \approx 5$ mm have $p = 0$ and not navigable by flight.

Probability of Passage

By summing experimental void passage numbers over time, we create curves for $E_r(t)$ which show graphically the relative prowess of mosquitoes for locating each void. Accordingly,

$$E_r(t) = \frac{1}{N} \sum_{i=1}^t n(i), \tag{3}$$

where $N = 100$, the index i represents 1 – s intervals used in data recording, and $n(t)$ represents the number of passages which occur at any given time increment, with a value of 0, 1, or 2. Experimental curves formed by Eq. (3) are shown by the dashed lines in Fig. 6a. Since $N = 100$ for each D , these curves represent the experimental cumulative probability $P(t)$ a single mosquito will find the ZOA by time t .

If a mosquito can probe the net barrier for passage anywhere inside the area of possible occupancy, an analytical expression of $P(t)$ takes the form,

$$P(t) = 1 - (1 - p)^{t/\tau}, \tag{4}$$

where τ is the time interval between subsequent attempts at barrier passage and $p = p(A_p, D, w)$. The value of τ can vary greatly with a

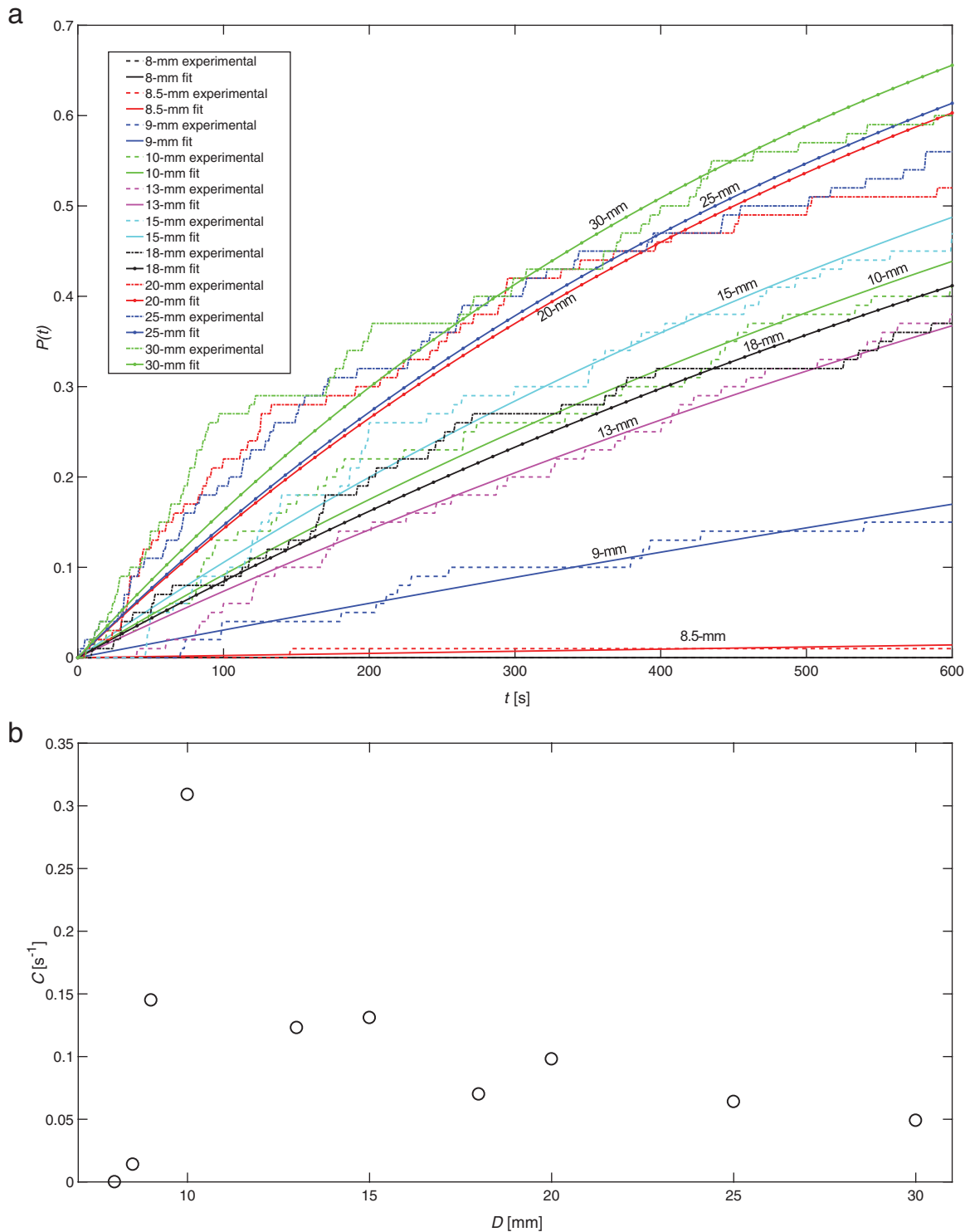


Fig. 6. (a) Cumulative rates of entry versus time, with respective curve fits for each void diameter tested. (b) Fitting parameter C versus void diameter D . Greater values of C represent greater proficiency in void finding.

single mosquito from multiple seconds to tenths of a second. Use of Eq. (4) assumes freedom to travel between any two points on the barrier between time steps of length τ and that probed locations have a completely random sequence. Thus, the mosquito must be able to achieve an average flight velocity of D_a / τ , which certainly is not possible for very large nets. The random walks of Fig. 4 have no pattern, but probed locations were clearly influenced by the

previously probed location. We do not expect the insect to probe two points a distance D_a from one another in subsequent time steps, for example. Additional complexity in predicting $P(t)$ is introduced by periods of rest, and the unknown and highly variant value of τ .

A slight modification of Eq. (4) allows for the collapse of unquantifiable behavioral influences into a single fitting parameter C , such that

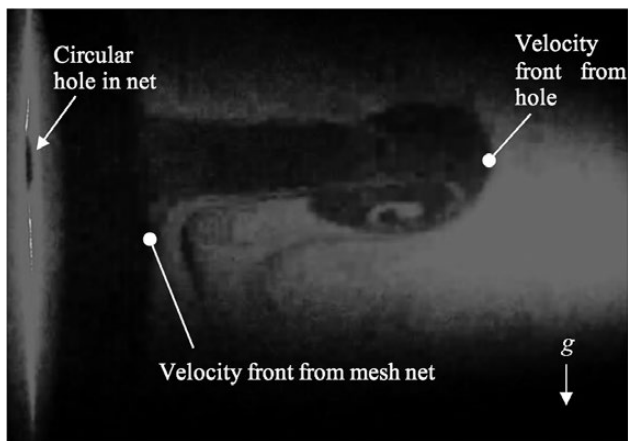


Fig. 7. Laser illuminated fog showing transient flow emanating from a 7-mm circular void in a bed net for forced airflow conditions. This image does not represent experimental conditions.

$$P(t) = 1 - (1 - p)^{Ct}. \quad (5)$$

We use Eq. (5) to fit the curves formed by Eq. (3) and likewise plot these in Fig. 6a. The fits of Fig. 6a are plotted on log–log coordinates in Suppl Fig. 5 (online only). Values of C and goodness of fit, R^2 , for each curve fit are listed in Table 1. A plot C versus D is given in Fig. 6b. The values of C represent the relative success of mosquitoes for locating a particular void. If translated into equivalent values of τ , we would have a range of $\tau = 3.2 - \infty$ s. Although not having the highest value of E_r , mosquitoes locate 10-mm void with the greatest ease relative to p . For this void, C seems anomalously high, and the cause for such a value is unknown. If performance across all void sizes was identical to that of the 10-mm void, we would expect $E_r(t = 600\text{s}) = 0.29 - 0.99$ for the experimental range of D . For voids larger than 10-mm void, the value of C gently declines. For $D \geq 9$ mm, the average value of $C = 0.124 \pm 0.082$ 1/s, which may be used to predict entry rates through void sizes and geometries not tested.

Discussion

In this study, we show the probability and relative ease of mosquito entry through a voided bed net. As evidenced by the values of C and E_r , void entry performance declines dramatically for $D < 9$ mm. The reason for this decline is unknown, but this surprising result may indicate an oversimplification in how we determine the p . Additionally, we do not consider encounters with the net to be oblique, which may weaken the probability of entry (see Suppl Movie 3 [online only]), and acknowledge our voids are not perfect circles due to the coarse weave of the net. However, for any void with $p > 0$, we do expect $E_r > 0$ if a greater number of individual mosquitoes are used. For voids smaller than $w/2$, the crawling mode of transport, which allows the mosquito greater conformation, may be used to defeat a barrier (see Suppl Movie 4 [online only]).

Our method for calculating p can be used to assign probabilities to noncircular voids. Under otherwise identical conditions, we expect values of C for noncircular voids to be close to the mean value of $C = 0.124$. For arenas of differing dimensions or for other insect species, the value of C could change dramatically. For example, houseflies *Musca domestica* Linnaeus (Diptera: Muscidae), in our experience, do not actively fly in a closed container and so the value of C would greatly depend on their crawling mechanics. In contrast, the orientation of the voids and their shape will modify only the value of p for airborne insects.

It is unlikely that greater test periods would result in dramatically different results. Mosquitoes are most active at the experiment's inception and activity levels decline with time as they tire and become desensitized to the attractant. In addition, the attractant scent gradient in the flight arena may become exceedingly weak as the scent is allowed to completely permeate the quiescent air in the arena volume. An avenue of future work would be the addition of a time-dependent term into Eq. (5) to refine passage probability estimates as activity wanes with time. Though not quantified, we notice mosquitoes tend to aggregate, in the upper half of the circular arena. Therefore, we surmise that placement of the void in the center of the barrier imparts no advantage for the mosquito. Void placement in the top half of the flight arena is likely to produce higher rates of escape. Accordingly, we expect voids placed at the bottom of the circular plane and at the bottom of deployed bed nets, present the lowest risk of mosquito entry.

The experimental values of C and E_r indicate the mosquitoes cannot visually detect and/or recognize voids. This is surprising since *Ae. aegypti* mosquitoes are known to be more attracted to some colors over others (Muir et al. 1992, Hoel et al. 2011). Black provides the greatest stimulus, and it would seem that a circular void would supply a stark light–dark contrast. While white is the least attractive color, it has not been shown to act as a repellent. The ability of visual detection would likely raise E_r nearly to 100% for any void with $P > 0$. The natural visual disguise of voids in nets increases the net's efficacy. Future researchers may search for weave patterns which further confuse or repel blood-seeking mosquitoes. However, lack of visual detection of voids does not preclude the attraction of mosquitoes to the void itself. Mosquitoes navigate odor plumes via gradients, or changes in scent concentration, rather than relying on absolute concentration (Geier et al. 1999, Dekker et al. 2001). Sutcliffe et al. (2017) report increased mosquito activity in the vicinity of larger voids (Sutcliffe et al. 2017), which may be a result of increased olfactory cues at the void when compared to the intact areas of the net. In our study, we saw greater E_r for $D = 10$ mm than for $D = 13.18$ mm, and little variation in E_r for $D = 10 - 18$ mm. While smaller voids carry a correspondingly smaller p , they may act to provide stronger olfactory gradients despite diffusion dominating scent transport. For forced flow, voids generate plume structures, as seen by the laser-illuminated transient flow shown in Fig. 7, generated by filling the flight tube with fog and starting a fan at one end. Air moves through the void with greater ease than the intact fabric. Plume structures and properties emanating from bed net voids are an area for future work.

Supplementary Data

Supplementary data are available at *Journal of Insect Science* online.

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